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Published in:
Behavioral Ecology and Sociobiology

DOI:
10.1007/BF00167742

Publication date:
1994

Behav Ecol Sociobiol (1994) 34:175–186

Behavioral Ecology and Sociobiology

Experimental evidence for helping and hindering by previous offspring in the cooperative-breeding Seychelles warbler *Acrocephalus sechellensis*

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Received: 9 July 1992 / Accepted after revision: 2 September 1993

Abstract. Prebreeding Seychelles warblers (*Acrocephalus sechellensis*) frequently act as helpers on their natal territory, aiding in territory defence, predator mobbing, nest-building, incubation (only females) and feeding dependent young of their parents. In some cases helpers could attain breeding status (e.g. by joint-nesting) in their natal group and become co-breeders. Comparisons of group size and reproductive success on a given quality territory suggest that the presence of alloparents (helpers and co-breeders) significantly affects the reproductive success of their parents. The influence of alloparents on reproductive success was examined by removing alloparents from breeding units and comparing the success of natural-sized and artificially reduced groups. Removal experiments, controlled for territory quality, group size and breeder age, showed that the presence of one alloparent significantly improved the reproductive success of its parents. Analysis strongly suggests that this was entirely due to helping behaviour (i.e. providing care to offspring of their parents), thereby improving the helper's inclusive fitness benefits from staying at home. However, these experiments showed also that the presence of two or more alloparents in medium-quality territories significantly decreased reproductive success, compared with groups with one alloparent. Several lines of evidence suggest that this may have been due to the joint-nesting and reproductive competition that could occur in breeding groups, or simply to resource depression when a large number of previous offspring remained on their natal territory.

Key words: Cooperative breeding – Alloparents – Experimental removal – Reproductive success – Social disruption

Introduction

Cooperative breeding is a reproductive system in which more than two parental adults provide care in the rearing of young. Such additional adults are called alloparents. These aid-givers may be non-breeding adults (usually called helpers), or co-breeders, sharing reproduction with other group members. The conspicuous helping behaviour of these helpers suggests that such activity enhances reproductive success in their social units, and it is often assumed that where improved reproductive output has been found amongst recipient breeders, the helpers have contributed significantly to the rearing effort (e.g. Emlen 1984). However, several authors have pointed out that enhanced reproductive success with increased number of helpers could be a by-product of some other relationship (Brown 1987; Koenig and Mumme 1990; Emlen 1991, Mumme 1992). For example, if good territories consistently enable breeding pairs to produce more young than poor territories, and if these young all remain on their natal territory for a year, then good territories will support larger groups than poor territories. Similarly, if breeding success is influenced by the age or past experience of the breeders, larger groups may form on the territories of such breeders. In either case, the presence of helpers would be an epiphenomenon of past successful breeding, and the positive correlation between number of retained young and unit reproductive success could be due to the effects of territory quality or breeder quality.

A more powerful test of the influence of helpers on reproductive success involves the removal of helpers from breeding units and directly comparing the success of natural-sized and artificially reduced groups. To date, three such experiments have been performed. The removals of helpers in the grey-crowned babbler (*Pomatostomus temporalis*, Brown et al. 1982) and in the Florida scrub jay (*Aphelocoma c. coerulescens*, Mumme 1991, 1992) led to decreased reproductive success, showing that helpers do actively help. No such effect was evident in a comparable experiment on the cooperatively breed-

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ing moorhen (*Gallinula chloropus*, Leonard et al. 1989). However, none of these experiments controlled for the effects of territory quality, group size and breeder quality, Clearly, additional experimental studies which control for the effects of confounding variables are needed (Brown 1987; Smith 1990; Emlen 1991).

In this paper I describe an experimental analysis of helping behaviour in the cooperatively breeding Seychelles warbler *Acrocephalus sechellensis*. At one time the total world population of this endemic warbler was reduced to 26 individuals, entirely confined to Cousin Island (29 ha) (Crook 1960). Following long-term management of Cousin by the International Council for Bird Preservation (ICBP, now called BirdLife International) since 1968, the warbler population made a spectacular recovery. Since 1982, the population has fluctuated around 300 birds (Komdeur et al. 1991; Komdeur in press). Given the vulnerability of one small island in the Indian Ocean, successful translocations of warblers to the islands of Aride (68 ha) and Cousine (26 ha) took place in September 1988 and June 1990 respectively, and the total population is now well over 500 individuals (Komdeur in press).

Once paired, warblers reside permanently in the same territories. The most common clutch size is a single egg (87.0%; $n=169$). Fledging occurs at 18–20 days, and young remain highly dependent on adults until they become proficient foragers at about 88 days of age (Komdeur 1991). Breeder mortality is low (18.5% per year) and divorce is rare, so the same pair occupies the same territory for several years, sometimes as long as 9 years. Although warblers can breed successfully in their 1st year, some individuals remain on their natal territories and delay breeding for several years, sometimes altogether. Cooperative breeding was first observed in a few high-quality territories in 1973 (Diamond 1980), when the number of territories reached its saturation level of circa 115 territories. Since 1982, it has been widely observed all over the island (Bathe and Bathe 1982). Group living is promoted not only by habitat saturation, but also by competition for higher-quality territories (Komdeur 1992). Groups consist of the breeding pair (which remain together as long as both birds survive), their dependent offspring (if they have recently bred successfully) and variable numbers of independent young from previous breeding attempts. On Cousin groups averaged 2.9 birds (range 2–12). Prebreeders could act as helpers on their natal territory, assisting in territory defence, predator mobbing, nest-building, incubation (females only) and feeding dependent young. Once they become helpers, they continued to help the same breeders throughout the time spent in the natal territory ($n=65$ helpers). Available evidence strongly indicated that in some groups it was not only the mated pair that could reproduce; extra-pair copulations, joint-nesting (where more than one female laid eggs in the same nest) and egg-removal could occur. In groups with one female and two or more adult males, 3 (15.0%) of the 20 observed copulations were by subordinate males. On one occasion a floating male was seen copulating with a nest-building female. Good proof of joint-nesting was that, in two groups of four females each, three and two, respectively, eggs were laid in one morning. In the same week these clutches were reduced to two and one egg respectively. The frequency of co-breeding is presumably low, as the commonest clutch size is a single egg, which was probably laid by the dominant female. When only one egg was present in groups of two to four individually known females ($n=17$), this was always laid by the mother (i.e. only she was on the nest half an hour before sunrise when the egg was laid). If observed genealogical relationships are sufficient to describe relatedness, assuming that the species is exclusively monogamous, then virtually all alloparents are grown offspring of both breeders (94.2%; $n=121$). The presence of alloparents therefore may affect the reproductive success of their parents.

This study was designed to answer two questions: (1) What are the mechanisms by which the presence of alloparents can affect the reproductive outcome of their parents? (2) Does the presence of alloparents change the reproductive success of their parents, independent of the effects of correlated variables such as territory quality, group size and parental quality? The removal of alloparents from breeding units enabled me to test whether the change in reproductive success of their parents is attributable to the presence of alloparents.

Methods

Study area

This study was conducted on Cousin Island in the Seychelles. The whole world population of Seychelles warblers (115–123 groups, 310–400 birds) was under continuous study between December 1985 and June 1991.

Data collection

Data presented here were based on individually colour-ringed birds. To record breeding activity and cooperative breeding all territories were checked every 2 weeks for active nests and presence of colour-ringed birds, the latter to determine the proportion of alloparents and breeders that died or survived to breed in another territory. Observations on nestbuilding, incubating, nest guarding (when bird was closer than 2.5 m to nest) and feeding young were made for 3 h comprising three 1-h segments equally spaced over the day: 0630–1030, 1030–1430 and 1430–1830 hours. Feeding observations started in the 2nd week after hatching and were repeated every 3 weeks until young died or reached independence. For each half minute it was noted whether or not each bird was taking part in each of the above mentioned categories. Incubation was measured at 110 nests. Total percentage incubation (i) in a group of n females incubating the same clutch was measured as:

$$i=\sum_{x=1}^{n}(i_x)-si$$

where i_x is percentage incubation by female x and si is percentage shared incubation at the same time by two or more females. Food provision frequency to nestlings was measured at 422 nests and total food provision frequency after fledging for 385 fledglings. Clutch size and number of nestlings were checked using an angled mirror attached to a pole. All nestlings were ringed with unique colour combinations and as many as possible were weighed at day 19 (fledging). Total food provision frequency to fledglings throughout the period of dependence was measured as the summa-

tion of mean food provision rates per 3-week intervals after fledging. As many fledglings as possible were caught and weighed in the 2nd month after fledging. On average fledglings appeared to be nutritionally independent by 3 months of age. Therefore the probability of reaching independence was measured as the probability of surviving the first 3 months.

In order to control for the effects of age on reproduction, only breeding pairs with both birds aged between 3 and 7 years were considered; this is the period during which annual reproductive success remained constant for both breeding males and females (Komdeur 1991).

Territory quality

Territory quality could be measured in terms of availability of nest sites, density of predators or food availability. Nest sites had no consistent features (within the same territory nests were found from 1 m to as high as 20 m) and were abundant. Adult Seychelles warblers lack natural predators. Nest-predators, Seychelles fodies (*Foudia sechellarum*) which are weaver birds endemic to the Seychelles, and two endemic skink species (*Mabuya wrightti* and *Mabuya sechellensis*), were evenly distributed over the island (Brooke and Houston 1983; Owen 1986). As the warblers are insectivorous, taking 98% of their insect food from leaves (Komdeur 1991), the quality of a territory depends on insect prey availability and foliage density. Territory quality (tq) was therefore expressed in terms of mean number of prey insects available using the following equation:

$$tq = a \sum_{x=1}^{12} (c_x i_x)$$

where a is mean annual territory size (hectares), c_x is mean yearly foliage cover for plant species x, and i_x is mean monthly insect totals for plant species x per unit leaf area (1 dm^2) in each year. Territory quality was studied monthly between May 1987 and June 1991.

To monitor effects of drought and wind direction on the vegetation, amount of foliage in each territory was measured using a transect method, during both the dry (May–September) and wet (November–March) season. The transect through each territory was 250 m long, subdivided into straight subtransects plotted 25 m apart from each other and facing north from one territory boundary to the other. Every 5 m the presence or absence of foliage and the plant species were noted in the following heights: 0–0.75 m, 0.75–2 m, 2–4 m, and at 2-m intervals thereafter. Total foliage cover for plant species x (c_x) is the total number of cases of presence of foliage at all heights along the transect.

To assess prey availability (i_x) in each territory, 50 leaves per plant species (12 dominant species) were searched for insects monthly (between 15th and 20th). Totals of the following groups were counted on upper- and under-sides: *Arachnida*, *Coleoptera*, *Diptera*, *Formicidae*, other *Hymenoptera*, *Hemiptera*, *Lepidoptera* and *Orthoptera*. In order to assess insect density for plant species x, the area of 250 leaves for each species was measured at 50 random sites on the island (five leaves per site).

Territories were divided into three categories: low quality territories (abbreviated lqt; tq = 0–15), medium quality territories (mqt; tq = 15–30), and high quality territories (hqt; tq = 30–45).

Removal experiments

The purpose of the removal experiments was to measure the effect of one (experiment I) and more than one (experiment II) alloparent on reproductive success of the breeders. Removal of alloparents was performed in 2 years of the 5-year study limited to young birds that were already known to have provided alloparental care. The remaining alloparents had provided alloparental care during the whole experimental period; both pre- and post-removal. The alloparents of both control and experimental units were fully related to the breeding pair (i.e. previous offspring).

Table 1. Mean annual territory quality (±SE) of control and experimental Seychelles warbler territories during (**A**) the 2-year period before and after the removal experiment in 1988, and (**B**) during the 2-year period before and 1 year after the removal experiment in 1990

Territory	Mean territory quality		*P*
	Pre-removal	Post-removal	
A. 1988			
Experimental (n)	15.6±1.4 (6)	17.8±2.2 (6)	NS
Control (n)	18.2±3.2 (9)	17.5±4.1 (9)	NS
P	NS	NS	
B. 1990			
Experimental (n)	21.6±3.9 (6)	20.2±4.3 (6)	NS
Control (n)	24.3±4.1 (6)	24.0±2.9 (6)	NS
P	NS	NS	

P values for territory quality differences between and within experimental and control territories determined by two-tailed Mann-Whitney *U*-test.
NS denotes $P > 0.05$ (n = number of territories)

Experiment I. In September 1988, 15 social units of Seychelles warblers containing an adult breeding pair and one alloparent were separated into groups of six experimental units and nine control units, both consisting of an adult breeding pair and one alloparent. From the experimental units the alloparent was removed and transferred to Aride Island.

Experiment II. In June 1990, 12 social units of Seychelles warblers occupying medium quality territories were separated into groups of six experimental and six control units. Of the six experimental units, three units had two, and three units had three, alloparents. All but one alloparent per unit were removed and transferred to Cousine Island. The control units, which were not manipulated, consisted of a breeding pair and one alloparent.

In both experiments, the annual reproductive success of each group was exactly known in the 2 years before and 2 years (Experiment I) or 1 year (Experiment II) after the removal experiment.

Territory quality, which was correlated with both reproductive success and unit size (Komdeur 1991), did not differ significantly between and within experimental and control territories during the experimental period (pre- and post-removal) (Table 1). In order to control for the effect of breeder experience, all adult pairs on the experimental and control territories had bred successfully (i.e. raised fledglings) before the experimental period. During the whole experimental period the dominant breeding pair and unit size (apart from the experimental reduction) remained the same, the ages of breeding birds remained within the 3–7 year age interval, and territory size of all considered units did not change significantly from year to year. Therefore the internal control used in this study (comparing reproduction pre-removal and post-removal on the same territory) is an explicit matched-pairs control for territory quality, group size, age and experience of the breeder.

Terminology

In this paper, I define a helper as "an individual that contributes physically, but not genetically, to young being reared". However, it is not possible to determine absolutely whether the dominant male or the dominant female always produced the offspring, i.e.

whether a helper was in fact a co-breeder. This study therefore will look at the effects of alloparents (helpers and co-breeders combined) on reproductive success of their parents. The estimation of the coefficient of relatedness between alloparents, breeders and offspring is based on genealogical data.

Statistical procedures

Statistical analysis was conducted using standard parametric and nonparametric techniques, including analysis of variance (ANOVA), multiple regression and logistic regression analysis to deal with multiple variables. Values of predictor variables, controlled for confounding effects, are presented as adjusted means (±SEs for the adjusted means) in figures. I have employed matched-pairs statistical tests to test the change in offspring production pre- and post-removal. When appropriate, I used one-tailed procedures to test specific hypotheses about the effect of alloparents on reproductive success and related aspects of breeding biology and behaviour. When not specified in the text, values of statistical tests are reported in the legends of figures or tables.

Results

Effects of alloparents on the annual number of young produced

In the Seychelles warbler, the relationship between number of feeders per group and reproductive success, controlling for age of the bird and territory quality, showed a step function (Fig. 1). Assuming that the average coefficient of relatedness (r) between alloparents and young is the same as that between parents and young ($r \approx 0.5$), the change in offspring production is a direct measure of the indirect fitness component of the alloparent.

One alloparent added to a pair occupying a low-, medium- or high-quality territory was associated with respectively 1.2, 2.8 and 1.3 as many fledglings as an unaided pair, which corresponded with 0.10, 1.54 and 0.35 additional juveniles respectively. The effect of an alloparent was even more pronounced in the annual number of fledglings surviving to one year of age. Groups with one alloparent produced 1.6, 3.0 and 1.6 times as many yearlings as those of unaided pairs for lqt, mqt and hqt respectively, which corresponded to 0.12, 1.00 and 0.58 yearlings per alloparent. A second alloparent apparently decreased reproductive success of groups occupying lqt and mqt, but produced 1.3 as many yearlings as groups with one alloparent of hqt. This corresponded to −0.04, 0.27 and 0.51 yearlings per alloparent. A third alloparent apparently had a negative effect on reproductive success of all social units.

Mechanisms accounting for the alloparental effects on reproductive success

In cooperative breeders, the changes in reproductive success with increasing number of alloparents could arise directly from alloparental care (hypothesis 1), or result from the incidental effects of group living, such as improved antipredator behaviour and territorial defence

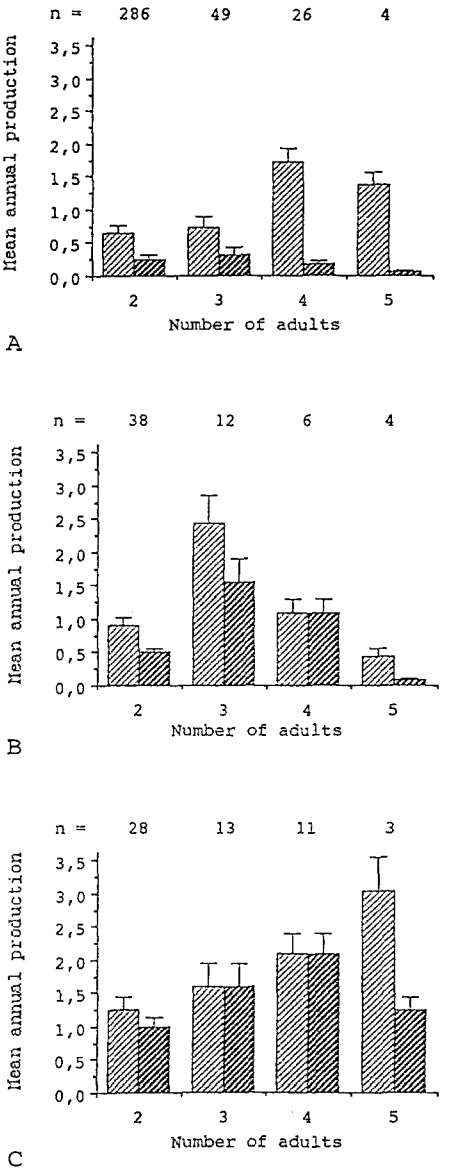


Fig. 1A–C. Mean annual production of fledged young (±SE) (*lighter shading*) and mean annual number of fledglings reaching 1 year of age (±SE) (*darker shading*) in social units of the Seychelles warbler in **A** low, **B** medium and **C** high quality territories. *Number of adults* is the breeding pair plus alloparents, who delivered food to young (n = number of territory years, 1986–1990). ▨ Annual production of fledglings; ▨ annual production of fledglings reaching one year of age

on the one hand, but more rapid resource depletion on the other hand (hypothesis 2, Koenig and Mumme 1990). Since alloparental care is not more likely to occur when breeding pairs produce more young, it is not necessary to control for such factors in considering the design of removal experiments.

Since all components of reproductive success in the Seychelles warbler (from annual number of nest-building attempts to annual number of fledglings produced) are auto-correlated (Komdeur 1991), mean fledgling production can be used as a measure to assess alloparental and group-living effects. In groups of one breeding pair

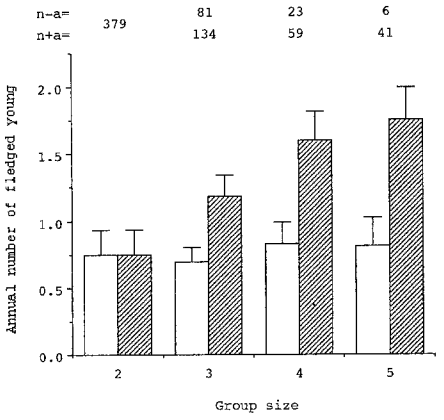


Fig. 2. Alloparental effects and group-living effects (without alloparental care) on mean annual production of fledged young in social units of the Seychelles warbler (1986–1990). Values presented are adjusted means calculated using analysis of variance in which the effect of territory quality was controlled ($n+a$ and $n-a=$ number of territory years for groups with (*shaded bars*) and without (*open bars*) alloparents respectively). ▨ Groups with alloparents: $r=0.99$, $df=611$, $P<0.001$, annual number of fledged young = 0.37*(group size)+0.02; □ groups without alloparents: $r=0.08$, $df=487$, $P=0.093$, annual number of fledged young = $0.04*10^{-1}$*(group size)+0.74

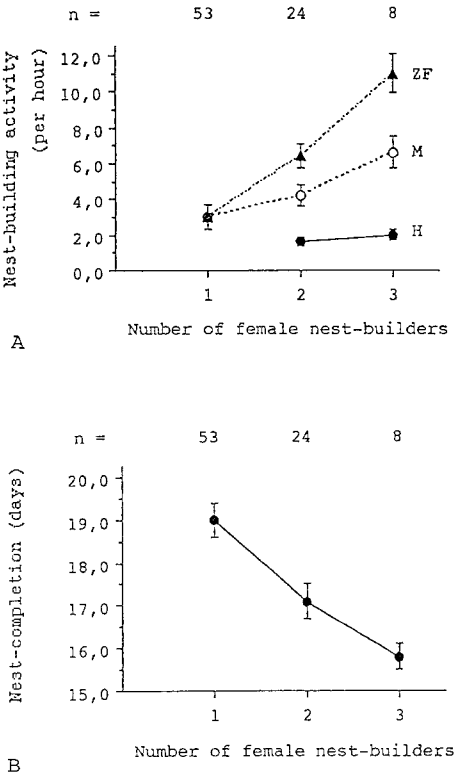


Fig. 3A, B. The effect of female helpers in the Seychelles warbler on **A** nest-building activity (number of half minutes spent nest-building per hour) by all females (*ZF*); nest-building activity by mother (*M*) and nest-building activity per helper (*H*) and **B** time taken (days) for nest-completion. Values presented are adjusted means (±SE) calculated using analysis of variance in which the effect of territory quality was controlled (n=number of nests, 1986–1990). **A**, *ZF*: $F=17.11$, $df=2$, $P<0.001$; *M*: $F=3.92$, $df=2$, $P<0.025$; *H*: $F=0.64$, $df=1$, $P=0.432$. **B**, $F=14.42$, $df=2$, $P<0.001$

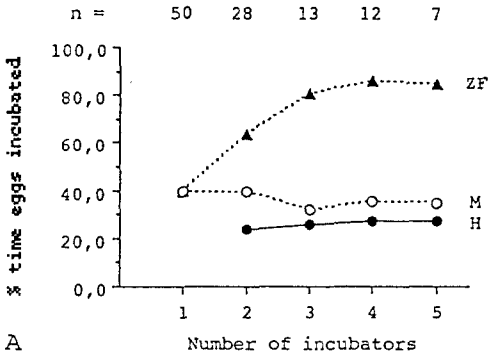
and several alloparents, which provided alloparental care, annual fledgling production increased significantly with group size, whereas in groups of one breeding pair with associated birds which did not provide alloparental care, reprodcutive output did not increase with group size (Fig. 2). Because alloparents are not more likely to help when the breeders produce more young, the comparisons in Fig. 2 show the direct effect of helping. The regression slopes of the two lines are significantly different ($t=25.0$, $df=1098$, $P<0.001$) and the fact that reproduction increases only with an increase in number of alloparents in the group clearly supports hypothesis 1. It is evident that the change in reproduction is really due to alloparentyl care per se, and not simply to the incidental effects of group living or to a higher reproduction rate by the breeders.

There are several ways in which alloparents could increase the reproductive success of their parents: (1) by bringing nesting material; (2) by incubation; (3) by feeding and tending the young both as nestlings and as fledglings. Generally by sharing costs of breeding the success of breeding attempts could be increased. This section examines the effect of alloparents upon the success of nesting attempts at different stages from nest-building to young reaching 1 year of age.

Effects of female alloparents on nest-completion. In the Seychelles warbler nest-construction was performed mostly by females. Female alloparents contributed significantly to nest-building (Fig. 3A), and nest-building rates increased significantly with number of nest-builders. As a consequence the time necessary for nest completion (the number of days between the onset of nesting and egg laying) was significantly reduced (Fig. 3B). However, after controlling for the effects of territory quality, the number of birds contributing to building the nest did not affect the probability that the nest would contain a clutch ($\chi^2=0.05$, $df=1$, $P=0.820$).

Effects of female helpers on hatching success. Between two and five females incubated a single clutch, and sometimes five birds were seen sitting on top of each other in the same nest. The mother, when she was assisted in nest-building, always incubated the clutch ($n=62$).

Total percentage of time when eggs were incubated increased significantly with number of incubators (Fig. 4A). However, increased hatching success was not correlated with the number of female incubators. The more incubating females, the higher the probability of two or more females incubating simultaneously (Fig. 4B). Females usually sat on top of each other, with the uppermost birds attempting to get down close in order to incubate the egg. The result of these movements and the extra weight in the nest resulted in a higher risk of nest loss from the tree with increasing group size (Fig. 4C). The presence of one female alloparent improved hatching success, but more alloparents appeared to be a hindrance (Fig. 4D). Hence, overall, mean



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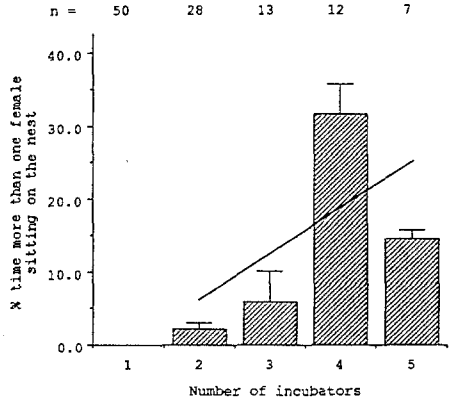

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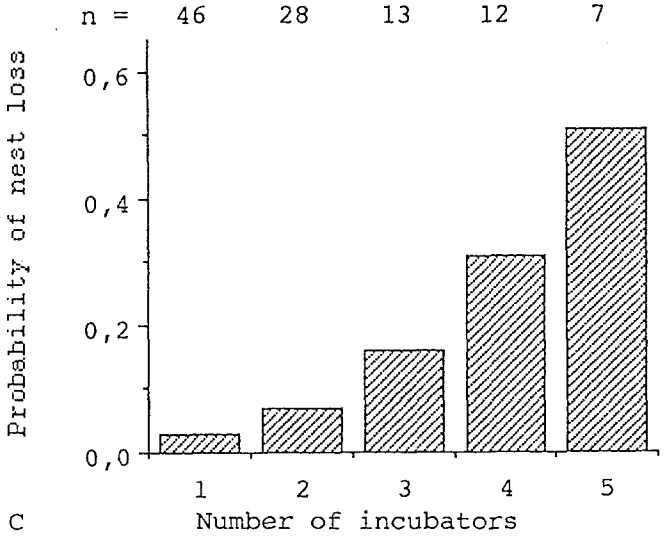

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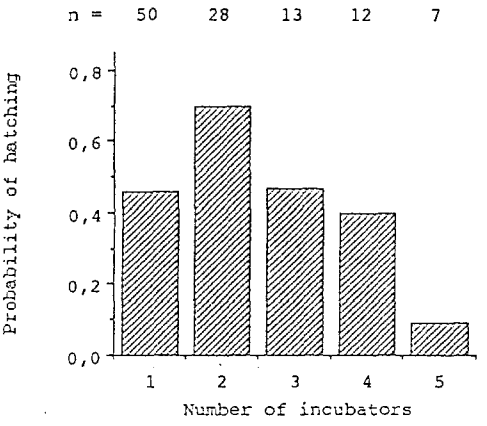

D

Fig. 4A–D. The effect of female incubators in the Seychelles warbler on: **A** percentage incubation by all females (*ZF*); percentage incubation by mother (*M*) and percentage incubation per helper (*H*); **B** the percentage shared incubation at the same time by two or more females ($n=110$ observed nests, 1986–1990); **C** probability of nest loss (n=number of observed nests, 1986–1990); and **D** probability of hatching. Values presented in **A** are adjusted means calculated using analysis of variance in which the effect of territory quality was controlled. Values presented in **D** are adjusted means calculated using logistic regression analysis in which the effect of territory quality was controlled (n=number of observed nests, 1986–1990). **A**, *ZF*: $F=68.17$, df=4, $P<0.001$; *M*: $F=1.37$, df=4, $P=0.252$; *H*: $F=1.32$, df=3, $P=0.283$. **B**, $r=0.65$, $df=108$, $P<0.001$, % time more than one female sitting on the nest = 6.56*(number of incubators) − 7.56. **C**, $\chi^2=15.08$, $df=1$ $P<0.001$. Probability of nest loss $=1/(1+e^{-z})$; $z=0.87$*(number of incubators) − 4.27. **D**, $\chi^2=11.09$, df=2, $P=0.029$. Probability of hatching $=1/(1+e^{-z})$; $z=0.13$*(territory quality) − $0.02*10^{-1}$*(territory quality)^2 + 2.52*(number of incubators) − 0.40*(number of incubators)^2 − 4.44

hatching success with alloparents was the same as without (mean: 46.0% ($n=50$) vs. 48.3% ($n=60$), $\chi^2=0.003$, $df=1$, $P=0.958$).

Effects of alloparents on fledging success. There was a significant increase in total feeding rate for all brood-sizes with number of alloparents, but with increasing brood-size, individual young were fed significantly less as food had to be shared between more young (Fig. 5A).

Total food deliveries to the single pulli increased by 35.7% with the addition of one alloparent, but remained the same with the addition of further alloparents, suggesting that the food needs of the young were being met with one or more alloparents. A significant proportion of the deliveries of food to nestlings came from alloparents (Fig. 6), on average 38.1% of the total ($n=155$ alloparents). The feeding rate per alloparent showed no decrease with increasing number of alloparents. Similarly, the breeding female's feeding rate remained constant with increased contribution from alloparents. However, the breeding male's contribution was significantly reduced with increasing number of alloparents (Fig. 6). The observed increase in feeding rate to single pulli with presence of alloparents was associated with a significant increase in fledging weight (Fig. 7). On average, body weight at fledging increased by 9.1% with the addition of one feeder, but remained the same with additional feeders. The increase in weight in the presence of feeders was associated with an increased probability of fledging (Fig. 8A).

The observed decrease in feeding rate with brood-size, however, was associated with a significant decrease in fledging weight; single pulli were 2.6 grams (18.7%; $n=75$) heavier than twins ($n=32$) and 3.9 grams (31.0%) heavier than triplets ($n=18$). This extra weight may enhance survival during the period from fledging to independence, when the young would be fed less and forage for itself. Overall fledging success showed a significant increase with number of feeders (Fig. 8A). Despite the observed decrease in feeding rate with brood-size, the probability of fledging as a pullus from multiple broods with number of feeders was the same as for a single pullus.

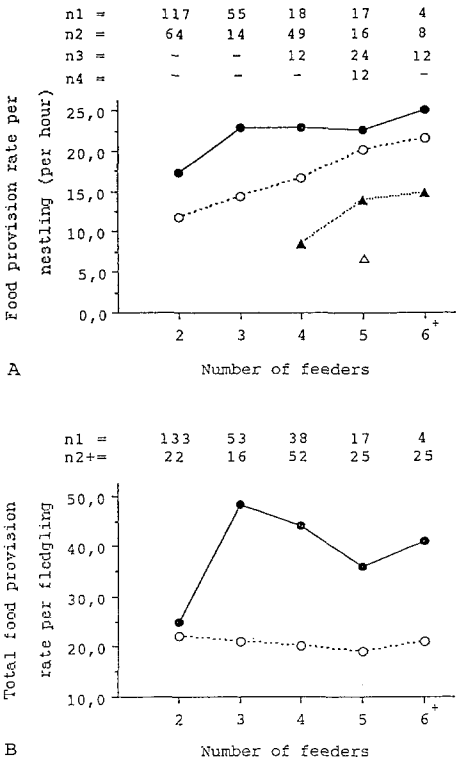

Fig. 5A, B. The effect of feeders and bood-size in the Seychelles warbler on **A** food provision rate per nestling and **B** total food provision rate per fledgling. Values presented are adjusted means calculated using analysis of variance in which the effect of territory quality was controlled (*nx* = number of observed young for brood-size *x*, 1986–1990). **A**, *Brood-size*: —●— 1; ·····○····· 2; ·····▲····· 3; △ 4. F(feeders) = 34.54, df = 4, $P < 0.001$; F(brood-size) = 88.16, df = 3, $P < 0.001$. **B**, *Brood-size*: —●— 1; ·····○····· 2+. F(feeders) = 9.46, df = 4, $P < 0.001$; F(brood-size) = 33.62, df = 2, $P < 0.001$

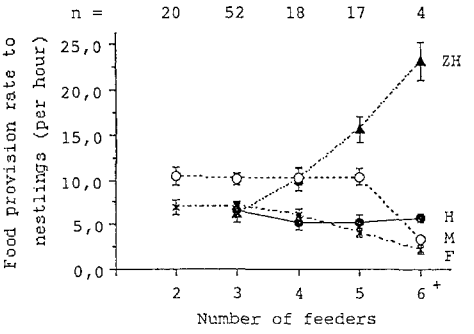

Fig. 6. The effect of feeders in the Seychelles warbler on food provision rate to nestlings from broods of one by all alloparents (*ZH*), by the mother (*M*), by the father (*F*) and per alloparent (*H*). Values presented are adjusted means (±SE) calculated using analysis of variance in which the effect of territory quality was controlled (*n* = number of observed young from broods of one only, 1986–1990). ·····▲····· ZH: F = 17.64, df = 3, $P < 0.001$; —●— H: F = 0.94, df = 3, $P = 0.433$; ·····○····· M: F = 2.20, df = 4, $P = 0.073$; ····· × ····· F: F = 7.05, df = 4, $P < 0.001$

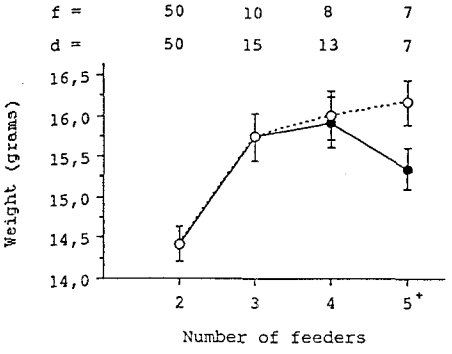

Fig. 7. The effect of feeders in the Seychelles warbler on fledging weight, measured at 19 days of age and on weight of young, measured between 2 and 3 months of age. Values presented are adjusted means (±SE) calculated using analysis of variance in which the effect of territory quality was controlled (*f* = number of young of 19 days of age, *d* = number of young between 2 and 3 months of age). Only young from broods of one are included (1986–1990). —●— weight (19 days): $F = 7.49$, $df = 3$, $P < 0.001$; ·····○····· weight (2–3 months): $F = 9.67$, $df = 3$, $P < 0.001$

Effects of alloparents on probability of reaching independence and one year of age. Fledglings from broods of one with three feeders received the most food. As for single pulli the observed increase in feeding rate was associated with a significant increase in fledgling body weight (Fig. 7). On average body weight increased by 9.2% with the addition of one feeder, but remained the same with additional feeders. The observed increase in weight with presence of feeders was associated with increased probability of reaching independence (Fig. 8B).

Young from larger broods were fed significantly less than young from broods of one (Fig. 5B), and had a significantly lower probability of surviving to independence (Fig. 8B). In contrast to the findings in the previous section, the probability of reaching independence for fledglings from larger broods showed a significant decrease with number of feeders. Annual survival of young from single broods showed a significant increase, but that of young from multiple broods remained constant with increasing numbers of feeders (Fig. 8C). More alloparents could therefore have a negative effect on annual reproductive success. This was due to the joint-nesting system, which resulted in more pulli per nest and hence more young to be fed. Fewer twins than singles reached independence and 1 year of age, and all triplets died before independence (Komdeur 1991).

Removal experiments

Effect of one alloparent on reproductive success (experiment I). Mean annual production of fledglings and yearlings was the same during the 2-year period before the experiment for experimental and control units, both consisting of the breeding pair and one alloparent (Fig. 9). After the removal experiment, reproductive success of the control group was the same as before, but there was a significant reduction in reproductive success of the reduced groups compared to the unreduced control groups (Fig. 9).

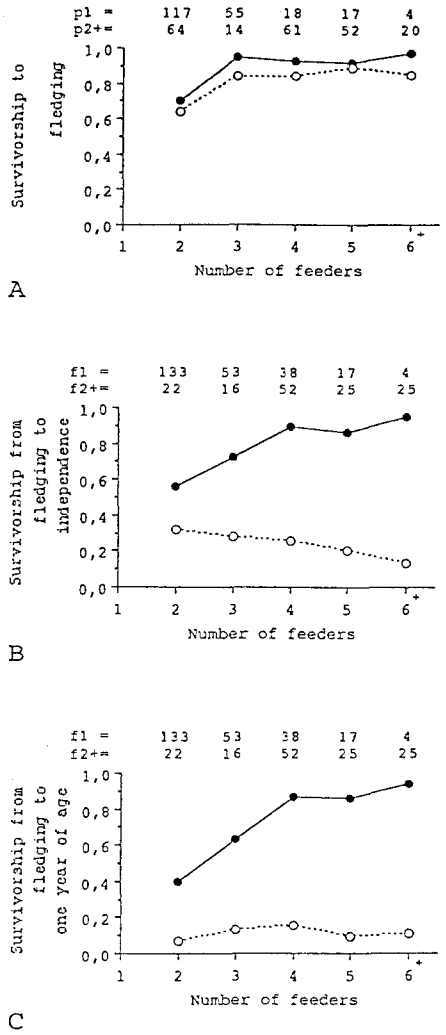

Fig. 8A–C. The effect of feeders and brood-size in the Seychelles warbler on **A** the probability of fledging, and on the probability of **B** reaching independence and **C** 1 year of age for fledglings. Values presented are adjusted means calculated using logistic regression analysis in which the effect of territory quality was controlled (*px* = number of observed pulli for brood-size *x*, fx = number of observed fledglings for brood-size *x*, 1986–1990). **A**, *Brood-size*: —●— 1 pullus; ·····○····· ≥2 pulli. χ^2 (brood-size) = 2.71, $df = 1$, $P = 0.100$. **B**, *Brood-size*: —●— 1 fledgling; ·····○····· ≥2 fledglings. χ^2 (brood-size) = 32,25, $df = 1$, $P < 0.001$. **C**, *Brood-size*: —●— 1 fledgling; ·····○····· ≥2 fledglings. χ^2 (brood-size) = 122.10, $df = 1$, $P < 0.001$

More detailed analysis of these data, broken down by components of reproductive success, indicates that the removal of alloparents did not have any significant influence on breeder survival, number of nesting attempts, percent of nests in which a clutch was laid, number of nests containing a clutch, clutch size, and the percentage of young surviving (Table 2). The increase in offspring production in the presence of one alloparent can be attributed to four factors (Table 2): (1) higher hatching success of eggs (increased by a factor of 2.2); (2) higher number of nests with nestlings (2.7×); (3) higher number of nests resulting in the production of fledglings (3.4×); and (4) 1-year-old young (5.2×).

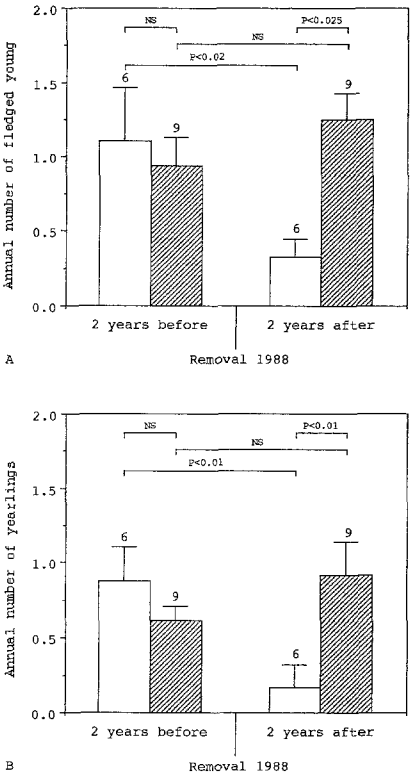

Fig. 9A, B. Reproductive success of experimental (one alloparent removed) (*open bars*) and unmanipulated control (*shaded bars*) groups of three Seychelles warblers (the adult breeding pair and one fully related alloparent) 2 years before (1986–1988) and 2 years after (1988–1990) the experimental removal. Reproductive success measured as **A** the annual number of fledged young and **B** the annual number of yearlings produced per group. Means, standard errors, and sample sizes are shown. *P*-values for differences between experimental and control groups determined by one-tailed Mann-Whitney *U*-test, and for pre- and post-removal by one-tailed paired-sample *t*-test. NS denotes $P > 0.05$. **A**, **B** □ Experimental; ▨ control

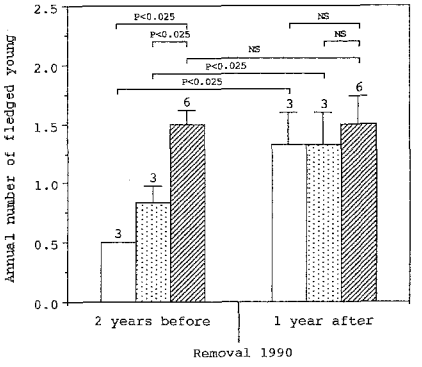

Fig. 10. Production of fledglings by experimental [one (*dotted bars*) or two (*open bars*) alloparents removed leaving the adult breeding pair and one fully related alloparent] and unmanipulated control units (*shaded bars*) of three Seychelles warblers (the adult breeding pair and one fully related alloparent) occupying medium quality territories 2 years before (1988–1990) and 1 year after (1990–1991) the experimental removal. Means, standard errors, and sample sizes are shown. *P*-values for differences between experimental and control groups determined by one-tailed Mann-Whitney *U*-test, and for pre- and post-removal by one-tailed paired-sample *t*-test. *NS* denotes $P > 0.05$. □ 2 Alloparents removed; ▩ 1 alloparent removed; ▨ control

Table 2. Effect of experimental removal of one alloparent in social units of three Seychelles warblers (the adult breeding pair and one fully related alloparent) on breeder survival, nesting, egg-laying, hatching and fledging success, and probability of reaching 1 year of age, 1986–1990

	Experimental groups ($n=6$)		P
	Pre-removal (1986–1988) (alloparent present)	Post-removal (1988–1990) (alloparent removed)	
% Breeder survival (n)	100 (12)	100 (12)	NS
Annual nest-building attempts			
Per group	2.11±0.88	1.83±1.21	NS
Total	38	22	
% Nests with clutch	68.4	63.6	NS
Annual number of nests with clutch			
Per group	1.44±0.68	1.17±0.37	NS
Total	26	14	
Mean clutch size (n)	1.08±0.27 (23)	1.00±0.00 (14)	NS
% Hatching success	92.3	42.9	$P<0.005$
Annual number of nests with pulli			
Per group	1.33±0.82	0.50±0.50	$P<0.005$
Total	24	6	
% Nestlings fledged	83.3	66.7	NS
Annual number of nests producing fledglings			
Per group	1.11±0.87	0.33±0.47	$P<0.02$
Total	20	4	
% Fledglings reaching one year of age	80.0	50.0	NS
Annual number of yearlings produced			
Per group	0.88±0.57	0.17±0.37	$P<0.01$
Total	16	2	

Statistical significance of comparisons determined by χ^2 contingency analysis (percentage data) or one-tailed paired-sample t-test. NS denotes $P>0.05$

Effect of two and three alloparents on reproductive success (experiment II). Before the removal of alloparents on medium quality territories, mean annual production of fledglings by groups with three alloparents was about half that of groups with two alloparents and one third that of groups with one alloparent (Fig. 10). The removal procedure reduced groups of three and two alloparents to just one alloparent. After the removal, mean annual production of fledglings by the experimental units increased significantly and was exactly the same as that in control units pre- and post-removal, comprising the breeding pair and one alloparent (Fig. 10). This permits matched comparisons between reproductive success of experimental groups pre- and post-removal.

The removal of alloparents (leaving the breeding pair and one alloparent) significantly increased reproductive success (Fig. 10). The removal of one alloparent caused a 1.6 increase in offspring production, whereas the removal of two alloparents caused an even higher increase of 2.7.

Full analysis of the fates of nest-buildings attempts by experimental groups before and after the removal experiment is shown in Table 3. These data indicate that the removal of alloparents did not have any significant influence on breeder survival, number of nest-building attempts, hatchability, number of nests containing a clutch or nestlings (Table 3). However, the increase in offspring production with the removal of alloparents (leaving one alloparent in the group) can be attributed to three factors (Table 3): (1) higher survival of clutches to hatching; (2) higher survival of nests with nestlings to fledging stage; and (3) higher number of nesting attempts leading to the production of fledglings; this was approximately twice as high for experimental groups after the removal experiment.

Nestling survival per nest and enhanced nesting success were associated with the removal of alloparents (Table 3). Although clutch size of experimental groups after the removal of alloparents was significantly lower, the numbers of nestlings and fledglings per nest were not significantly different from that of experimental groups after the removal. Percentage hatching success and percentage nestlings fledged were the same before and after the removal experiment.

Discussion

Removal experiments and social disruption

Experimental manipulations of group composition under natural conditions are generally viewed as a valuable but under-utilized technique among avian sociobiologists (Brown 1987; Smith 1990). Although controlled removal experiments of helpers can clarify hypothesized causal relationships and control for the effects of poten-

Table 3. Effect of experimental removal of one alloparent from social units of four and two alloparents from social units of five Seychelles warbler occupying medium quality territories on breeder survival, nesting, egg-laying, hatching and fledging success, and fate of clutches, 1988–1991

	Experimental groups ($n=6$)		P
	Pre-removal (1988–1990) (two/three alloparents present)	Post-removal (1990–1991) (one alloparent present)	
Breeder survival (a)	100 (12)	100 (12)	NS
Nest-building attempts			
Per group	2.83±0.47	2.50±0.58	NS
Total	34	32	
% Nests with clutch	70.6	62.5	NS
Number of nests with clutch			
Per group	2.00±0.29	1.67±0.37	NS
Total	24	20	
% Hatching success	75.0	100.0	$P<0.05$
Number of nests with pulli			
Per group	1.50±0.29	1.67±0.37	NS
Total	18	20	
% Nestlings fledged	61.1	95.0	$P<0.05$
Number of nests producing fledglings			
Per group	0.83±0.24	1.58±0.34	$P<0.01$
Total	11	19	
Fate of clutch			
Clutch size (n)	1.56±0.5 (9)	1.0±0.0 (9)	$P<0.05$
Hatching success	84.6 (13)	100 (9)	NS
Number of nestlings hatched per nest (n)	1.38±0.48 (8)	1.0±0.0 (9)	NS
% Nestlings fledged (n)	54.6 (11)	88.0 (9)	NS
Number of nestlings fledged per nest (n)	0.75±0.43 (8)	0.89±0.31 (8)	NS

Statistical significance of comparisons determined by χ^2 contingency analysis (percentage data) or one-tailed paired-sample t-test. NS denotes $P>0.05$ (a=number of breeding birds, n=number of nests observed)

tially confounding variables, they can still cause side-effects in the assessment of reproductive success of the reduced groups (Koenig and Mumme 1990). An alternative explanation for the experimental results presented here is the "social disruption" hypothesis (Mumme 1992). Perhaps the reduced reproductive success of the experimental groups is a result not of the absence of alloparental care per se but a result of the social disruption caused by removal of group members. For example, the lower reproductive success of experimental groups from which one alloparent had been removed (Fig. 9) may have been caused either by the absence of this alloparent, or by the social disruption caused by the removals.

However, as shown in Tables 1 and 2, the experimental removal of one alloparent had no adverse effect on territory size and hence indirectly on territory quality, breeder survival, annual nest-building attempts or annual number of nests containing a clutch. If social disruption were a significant problem, more immediate effects on reproduction would be expected. Moreover, as shown in Fig. 10 and Table 3, experimental removal of two or three alloparents can actually increase reproductive success. It is therefore unlikely that the differences in reproductive success between control and experimental groups were caused by social disruption, but rather that they are due to changes in alloparental care itself. This interpretation is also supported by Mumme (1992) in his experimental analysis of helper effects on reproductive success in the cooperatively breeding Florida scrub jay.

Is alloparental care beneficial?

Because of the possibility of multiple paternity and maternity, it was not possible to know whether the dominant male and the dominant female were always the genetic parents of the offspring, and hence whether a helper was in fact a co-breeder. There is clear evidence that the enhanced reproductive success observed in groups with one alloparent during the first experiment (Fig. 9 and Table 2) is attributable to helping effects only. In this experiment the average clutch size of experimental groups and control groups was one egg, which was probably laid by the dominant female, suggesting that the alloparents were genuine helpers, providing care to offspring of their parents (coefficient of relatedness between helper and offspring ≈ 0.5). Even so, despite the complications of co-breeding, the coefficient of relatedness between alloparent and offspring varies probably around 0.5, independent of whether it is the offspring of the parents or its own, because virtually all alloparents are grown offspring of both breeders ($r \approx 0.5$).

Although alloparents almost certainly incur some di-

rect fitness costs when they provide aid to nests and provision dependent young, these costs are probably small as these had no detectable effect on their survival. Survival from 2 to 3 years of age was the same for alloparents as for additional birds which did not provide alloparental care [84.9% ($n=33$) vs. 82,8% ($n=29$), $\chi^2=0.015$, $df=1$, $P=0.904$]. In contrast, the fitness benefits of alloparental care by alloparents can be substantial, controlled for potential correlated variables such as territory quality and parental quality.

This study has shown that experimental groups with one alloparent (most likely a nonbreeding helper) produce more offspring than do the same groups after removal of the alloparent. As the costs of helping are negligible, and helping does not influence breeder survival (Table 2), the increased reproductive success of groups with one helper is entirely the result of helping (Fig. 9). The presence of one helper increases the annual production by an average of 0.78 fledglings and 0.71 yearlings per group (Fig. 9). As the average coefficient of relatedness between these helpers and young is the same as that between parents and offspring, a single Seychelles warbler helper increases its fitness by an average of 0.71 offspring (yearlings) equivalents; a substantial supplement to the indirect component of a helper's inclusive fitness.

On the other hand, the second experiment showed that alloparental care by two or three alloparents (mean of 2.5 alloparents per group) decreases the productions of fledglings by an average of 0.67 young compared to groups with one alloparent (Fig. 10). On average, an additional alloparent decreases reproductive success by 0.45 offspring. The average inclusive fitness per alloparent in these groups is 0.13 [=(0.78–0.45)/2.5] fledgling equivalents only. This may simply result from the greater depletion of the food resource because of the presence of a larger number of previous offspring on a territory which is sufficient to reduce the reproductive success of the parents. However, several lines of evidence suggest that decreased reproductive success is due to co-breeding and reproductive competition that could occur in breeding groups. The presence of two or three alloparents significantly increased clutch size (Table 3), which may have been caused by joint-nesting by alloparents. Under natural circumstances breeding groups with two or more females, which all fed young at the nest, produced a significantly larger clutch size than a single breeding pair. Evidence exists that suggests this arises from more than one female laying eggs. In groups of one female and several males (which acted as helpers) clutch size did not increase with group size (Komdeur 1991). Hence it would appear that multiple maternity was responsible for enhanced clutch size rather than the dominant female adjusting clutch size to the potential helping power of known group size.

However, despite the larger clutch size there was no detectable effect of group size on number of nestlings fledged per nest (Table 3). This may have been the result of reproductive competition. Alloparents attempt to reduce the reproductive contribution of other group members by removing eggs from the nest (Komdeur 1991). Furthermore, more pulli per nest were produced in the joint-nesting systems (although not significantly in this experiment) and more young had to be fed. Consequently, these nestlings weighed less than an average single nestling, and had a lower chance of reaching independence and to one year of age.

The preceeding analyses strongly suggest that the presence of alloparents has a substantial effect on the indirect component of an alloparent's inclusive fitness. By comparing the fitness consequences of staying and helping versus dispersing and breeding in the Seychelles warbler (assuming that no breeding status was achieved by the helper within its original group), a one-year-old warbler could produce more offspring over its lifetime by remaining in a high quality territory for several years as a helper and then breeding, than it could by dispersing and breeding immediately in a lower quality territory (Komdeur 1992).

Acknowledgements. I thank Nick Davies for supervising this study and for his extremely constructive feedback during the early stages of the study. I am also grateful to Michael Rands (Deputy Director-General for BirdLife International), who set up the Seychelles warbler research program and arranged permission for the transfer, and John Neville for assistance on Cousin Island from September 1990 to June 1991. Helpful criticisms of an early draft of the manuscript were provided by Nick Davies, Ronald Mumme, Tony Fox and an anonymous reviewer. Financial support for the research and the transfer of warblers to Cousing Island was provided by the ICBP. I thank Christopher Cadbury for generously financing the transfer of warblers to Aride Island.

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